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Entomophily in *Waltheria indica* L. (Malvaceae), *Melastoma malabathricum* L. (Melastomataceae), *Mimusops elengi* L. (Sapotaceae)

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ABSTRACT

W. indica, *M. malabathricum* and *M. elengi* are seasonal bloomers but flowering and fruiting can occur year-long in *W. indica* and *M. malabathricum* if soil is wet. All three species are hermaphroditic and homostylous. *W. indica* and *M. malabathricum* are diurnal bloomers while *M. elengi* is a nocturnal bloomer. Anthers dehiscence is longitudinal in *W. indica* and *M. elengi* while it is poricidal in *M. malabathricum*. In *M. malabathricum*, heteranthery is functional with one set of anthers act as feeding anthers and another set as pollinating anthers. All three species are entomophilous; bees and butterflies in *W. indica*; bees in *M. malabathricum* and bees and wasps in *M. elengi*. Fruit is a 1-seeded dehiscent capsule in *W. indica*, many-seeded berry-like fleshy capsule in *M. malabathricum*, and 1-seeded fleshy bullet-shaped berry in *M. elengi*. Hydrochory, zoochory and anthropochory are functional in *W. indica*, ornithochory and hydrochory in *M. malabathricum* and ornithochory and chiropterochory in *M. elengi*.

Keywords: *Waltheria indica*, *Melastoma malabathricum*, *Mimusops elengi*, entomophily, heteranthery, seed dispersal.

1. INTRODUCTION

The genus *Waltheria* named after the German botanist August in Friedrich Walther (Quattrocchi, 2000) has 60 species of obligate heliophytes distributed in semiarid, coastal, riverine dunes and thorn-scrub habitats of sub-tropical and tropical regions with 53 species confined to Americas, 6 species to paleotropics and 1 species is pantropical. Paleotropical species are endemic to the Islas Marquesas and Society Islands, Madagascar, West Africa or Hainan Malaysia and Australia see (Saunders, 2011). Most species are shrubs or sub-shrubs that display flowering for several months in a year. They produce a few flowers in axillary or terminal clusters at each node and remain open for a day (Rzedowski, 1978). In this genus, approximately 40 species are reported to distylous with pin and thrum flowers produced on different individuals.

The production of an equal ratio of both flower forms in a population is reported to be an indication of the function of strong self-incompatibility system. In distylous species, distyly breaks down occasionally through recombination or by the function of modifier genes and production of homostylous populations that may contribute to species arise (Ganders, 1979). In this genus, three species groups, fan-plumose stigma type, elongate-plumose stigma type and crest-flowered waltherias type have been delineated based on certain characters such as stigma type, habit, pin pollen average aperture number and fruit aspects (Saunders, 1988). The fan-plumose stigma group involves the presence of fan-plumose stigma in both pin and thrum flowers, production of spirally disposed leaves and completely or partly bony, bivalvate capsules. The elongate-plumose stigma group involves the presence of elongate-plumose stigmas in both pin and thrum, bracts presenting simple trichomes on the adaxial surface and gland-tipped trichomes on both surfaces. The crest-flowered waltherias group involves the presence of crest-like inflorescence, clavate pin stigmas and an ovoid chartaceous capsule with partial loculicidal capsule dehiscence along the suture from the placenta upward and across the apical portion and down a short distance on the oblateral side (Saunders, 1993).

Little information is known about pollination aspects of *Waltheria* species. Schofield, (1989) stated that *W. ovata* distributed in Galapagos Islands and South America is mentioned by previous workers as homostylous but his study found that this species in the same distribution area is distylous. Hervias-Parejo and Traveset, (2018) reported that *W. ovata* is entomophilous but pollination effectiveness is more when pollinated also by birds. Costa et al., (2002) reported that *W. cinerascens* is distylous and pollinated by the carpenter bee, *Xylocopa cearensis*. The foraging behaviour of this bee facilitates intermorph pollination in this plant species in Brazil. Rodriguez-Parilli and Graterol, (2011) reported that *W. americana* in Venezuela is visited by several bee species. This plant has great potential for managing the bee fauna in agricultural ecosystems. Saunders, (1993) reported that *W. indica* represents fan-plumose stigma group. Different authors reported that *W. indica* is homostylous in Paraguay (Saunders, 2007), Central America (Tropical Plants Database Ken Fern, 2022), China (Hsiang-hao, 1984) and India (Sharma and Sanjappa, 1993). But, Bir Bahadur and Srikanth, (1983) reported that *W. indica* has heterostylous self-incompatible and homostylous self-compatible forms in India. Heterostyly is functional through distyly with pin and thrum flower morphs produced on different individuals. Heterostylous populations are confined to certain isolated pockets of Andhra Pradesh and Tamilnadu. The function of heterostyly is stated to be representing an isolating mechanism of pre-zygotic type. Homostylous forms represent Chilkur and Local populations the former type is endemic to Chilkur forest in Andhra Pradesh while the latter type has worldwide distribution. Chilkur homostylous form is stated to be a consequence of mutation or crossing over from parental heterostylous forms in the distant past and this form remained isolated from heterostylous and local homostylous populations. Local homostylous population might have given birth in the distant past because self-compatibility facilitates to produce populations even isolated habitats and enables it to be a weedy species to have wide distribution and establishment. These authors also stated that heterostylous and homostylous forms do not cross with each other in areas due to their mechanical and geographical isolation. Finally, it is documented that the distylous *W. indica* is the original species while the homostylous forms of this species need to be classified as two different species.

Melastomataceae family has more than 4000 species in the tropical and subtropical parts of the world. In this family, *Melastoma* genus has 22 species, 2 sub-species and 3 varieties in the Southeast Asian region alone (Rajenderan, 2010). The word “melastoma” is a Greek word for “black mouth”, a name for black color tongue in people who eat the berries (Koay, 2008). *M. malabathricum* is reported to have 2 sub-species, *M. malabathricum* ssp. *malabathricum* and *M. malabathricum* ssp. *normale* (Meyer, 2001). This species is cultivated due to its ornamental and medicinal value (Neal, 1965). In Melastomataceae, most species produce poricidal anthers and are buzz-pollinated by pollen collecting bees through sonicating the anthers with the aid of their indirect flight muscles (Buchmann, 1983; Renner, 1989; King et al., 1996). In this process, bees directly land on the stamens, grasp them securely and firmly with their legs and then employ high frequency vibrations to expel pollen from the anther through their apical pores.

Melastoma malabathricum is native to tropical and temperate Asia and the Pacific Islands (Ling et al., 2009) but it is distributed in the Indian Ocean Islands, South and South-east Asia, China, Taiwan, Australia and the South Pacific Ocean (Wong, 2008). *M. malabathricum* is a known hyperaccumulator of aluminium and as such can be used for phytoremediation (Watanabe et al., 1998). Lu et al., (2009) reported that *M. malabathricum* is facultative xenogamous. Its flowers display heteranthery with color dimorphism; two sets of stamens each set with a different color. One set of stamens are yellow and serve to attract pollinators and satisfy their demand for pollen. Another set of stamens are purple and satisfy the plant's requirement for safe pollen dispersal. Both sets of anthers do not show any difference in pollen viability, histo-chemistry and fruiting rate.

Very little is known about floral and pollination aspects of Sapotaceae family. In *Pouteria* and *Magodendron*, the flowers have a nectary disk but it is nectarless. *Manilkara fasciculata* is visited by bees (Marshall and Beehler, 2011). *Chrysophyllum roxburghii* is pollinated by insects (Wiselius, 1998). The genus *Mimusops* with 57 is native to tropical and subtropical parts of Asia, Africa, Australia and oceanic islands (Allaby, 1998; Govaerts et al., 2002). There is absolutely no information the pollination ecology of this genus. Reddi and Janaki Bai, (1981) reported that *M. elengi* flowers display nocturnal anthesis and emit very strong fragrance; they

do not have nectar disk but nectar is produced around the ovary. The floral traits indicate that this species is mostly likely anemophilous. These authors also mentioned that bees visit the flowers of this species but they do not have any role in pollination.

With this backdrop, the present study was carried out to describe certain details of pollination ecology of *Waltheria indica*, *Melastoma malabathricum* and *Mimusops elengi* for which there is little information is available to understand their sexual reproduction. The outcome of the study is explained in the light of relevant published information to a fruitful end.

2. MATERIALS AND METHODS

Waltheria indica growing in Rushikonda area, *Melastoma malabathricum* at G. Madugula wild pocket and *Mimusops elengi* in Visakhapatnam Urban Development Park in Visakhapatnam District, Andhra Pradesh, India was chosen for the present study during June 2021 to June 2022. All three plant species were observed in the areas where they grow to record their flowering period, anthesis and anther dehiscence mode. The flowers were observed for their floral biology and the details were recorded. Flower visitors on each plant species were insects and they were observed for their daily foraging schedule and probing behavior for forage collection in effecting pollination. Since all the three plant species are hermaphroditic, all fertilized flowers set fruits. Fruit characters and fruit maturation time along with seed aspects were also recorded.

3. OBSERVATIONS AND DISCUSSION

Waltheria indica

It is a small perennial softly pubescent herb with erect or spreading branches and simple petiolate elliptic pubescent leaves with alternate arrangement (Figure 1a). It flowers and fruits throughout the year in wet areas while it shows intense flowering and fruiting during July-December. The flowers are open from morning to early afternoon. The flowers are sub-sessile born in axillary and terminal cymose clusters, bright yellow, faintly odoriferous, nectariferous, bi-sexual, homostylous and zygomorphic. The calyx has 5 green triangular sepals fused basally and free apically. The corolla has 5 yellow spatulate petals. The stamens are 5 each with dithecal anthers, connate at base enclosing the ovary and arranged opposite to petals. The ovary is sessile, globular, 1-celled with 2 ovules and extended into a prominent style tipped with a feathery stigma.

Hervias-Parejo and Traveset, (2018) reported that *W. ovata* is entomophilous but pollination effectiveness is more when pollinated also by birds. Costa et al., (2002) reported that *W. cinerascens* is distylous and pollinated by *Xylocopa cearensis*. Rodriguez-Parilli and Graterol, (2011) reported that *W. americana* is visited by several bee species. Saunders, (1993) reported that *W. indica* represents fan-plumose stigma group. *W. indica* is homostylous in Paraguay (Saunders, 2007), Central America (Tropical Plants Database Ken Fern 2022), China (Hsiang-hao, 1984) and India (Sharma and Sanjappa, 1993). But, Bir Bahadur and Srikanth, (1983) reported that *W. indica* has heterostylous self-incompatible and homostylous self-compatible forms in India. Heterostylous form is confined to certain isolated pockets of Andhra Pradesh and Tamilnadu and pollinated mostly by thrips and certain butterflies. Homostylous forms represent Chilkur and Local forms the former type is endemic to Chilkur forest in Andhra Pradesh while the latter type has worldwide distribution. In this study, *W. indica* is a homostylous self-compatible form. Its flowers were foraged by the honey bee, *Apis cerana* (Figure 1b) for pollen and nectar and the butterflies, *Pachliopta aristolochiae* (Figure 1c), *Papilio crino* (Figure 1d) (Papilionidae), *Delias eucharis* (Figure 1e) (Pieridae) for nectar during daytime with intense foraging visits from 1100 to 1500 h. All these foragers were consistent in their foraging activity and exhibited fidelity to this floral source during intense flowering period. Since the flowers are borne in clusters at each node, a visiting bee or butterfly has the advantage of visiting several flowers in the same or different clusters of the same plant by minimizing the flight time and search time. As a result, such a floral arrangement is also advantageous for the plant to maximize the pollination rate by producing minute volume of nectar. Self-compatibility functional in this species by the placement of stigma and anthers nearly at the same height enables it to resort to spontaneous autogamy and build up its populations in the existing or new habitats with or without insect pollination. Therefore, the hermaphrodite sexual system with homostyly and self-incompatibility functional in *W. indica* ensures it to become a successful weed and is attested by its pantropical wide distribution.

The fruit is a small, round dry dehiscent 1-seeded capsule. The seeds released from the capsule are dispersed by rain water and grazing animals and even by agricultural equipment in croplands. Since seed dispersal is mediated by three different modes, this plant has huge opportunities to migrate, settle and establish population in various ecological habitats.



Figure 1 *Waltheria indica*: a. Habit, b. *Apis cerana* collecting nectar, c. & d. Papilionid butterflies – c. *Pachliopta aristolochiae*, d. *Papilio crino*, e. Pierid butterfly, *Delias eucharis*.

Melastoma malabathricum

M. malabathricum is an evergreen shrubby spreading weed (Figure 2a). The stem is erect with slender branches, tetragonal and covered with ciliate scales. The leaves are petiolate, stiffly papery and elliptic with pointed tip. The inflorescence is a terminal corymbose raceme with 3-8 flowers. The flowering occurs throughout the year but it is profuse during wet season. The flowers are arranged in around 1-5 flowered clusters (Figure 2b). The flowers show variation from light to dark pink. The calyx is campanulate with 5 ovate-lanceolate pubescent hairy lobes with acuminate apex. The petals are five, reddish purple and obovate. The stamens are 10 of two different kinds, 5 each in outer and inner whorls. The outer whorl stamens are long and have straight yellowish-white part and upper curved purple part, two short yellow horns are present at the junction of joining of two parts, the end of curved filament has purple anther. The short stamens have yellow filaments and anthers and placed in center of the flower. The anthers of both long and short stamens dehisce poricidally and the pores at their tips can be seen, through which pollen grains liberate when triggered by the wing vibrations of appropriate flower-visiting insect, especially specialized bees. The purple stamens produce relatively more pollen than yellow stamens; all ten stamens produce fertile pollen. The ovary is 5-locular with many ovules tipped with a ring of setae apically and springs up from the center; it is extended into a long pinkish style with a green capitate stigma. The flowers are ephemeral and remain in place for a day or two only.

Mature buds begin to open at dawn and unfold petals completely exposing the sex organs after sunrise. At this stage, the stamens of outer whorl drift to the lower portion of the flower by gravity to result in asymmetric androecium. The flowers offer only pollen as reward to foraging insects. Although all ten stamens produce fertile pollen with similar characters, the yellow anthers of inner stamens appear to act primarily as feeding anthers while the purple anthers of outer stamens act as pollinating stamens. The yellow anthers also appear to have a specific role in attracting the pollinator insects from a distance. Gross, (1993) reported the function of bimorphic anthers in *M. malabathricum*. He stated that the yellow stamens function mainly as feeding anthers while purple stamens as pollinating anthers. Further, yellow stamens also serve as attractants to draw the attention of foraging insects.

In this study, carpenter bees of the genus *Xylocopa latipes* and *X. pubescens* and the sweat bees of the genus *Nomia* sp. (Figure 2c, d) were the regular foragers throughout the day with intense pollen collection activity during 1100-1500 h. The carpenter bees displayed similar behavior to collect pollen. Usually, they landed on the yellow anthers, grasped them individually or collectively and buzzed for 2-4 seconds to milk pollen from the anthers with their mandibles. In this process, the apical portion of purple anthers contacted the sides and abdomen of the carpenter bees while the apical parts of the yellow anthers were positioned close to the mouth parts of these bees. The clouds of pollen ejected from the apical pores of the purple stamens settled on the dorsal and ventral side of the abdomen of the bees. The abdomen portion of the bee body touched the stigma during subsequent visit(s) to next visited flowers. As a result, pollen is transferred effecting self-or cross-pollination. The sweat bees also landed directly on the yellow anthers but they did not make any buzzes to collect pollen; they simply extracted pollen accessible in and around the rim of yellow as well as purple anthers with their mandibles. The pollen-laden ventral side of these bees touched the stigma of flower(s) that were visited by them in succession and effecting pollination. Gross, (1993) noted that *M. malabathricum* is self-compatible which facilitates the occurrence of self-pollination assisted by pollen vectors. In this context, it is reasonable to state that *M. malabathricum* achieves both

self- and cross-pollination by carpenter bees. Other bees such as sweat bees as recorded in this study serve effect additional pollinations and hence act as supplementary pollinators. Different workers reported that color dimorphism with stamens in flowering plants is not uncommon and its presence and function relates to deception of flower visitors by brightly coloured anthers, but rewardless decoys (Percival, 1965; Mattsson, 1976; Vogel, 1978; Bahadur et al., 1996; Hrycan and Davis, 2005).

In the present study, *M. malabathricum* flowers produce fertile pollen in yellow (feeding) and purple (fertilization) anthers, the former type is intended to provide sufficient pollen to attract efficient pollinators, in this case, carpenterbees to receive enough pollen to pollinate all ovules produced in an ovary while the latter type is intended for buzzing by the bees for the flower to transport pollen to other flowers. Further, the function of dimorphic anthers is related to the small diameter of anther pore for pollen ejection in a precise manner onto specific body parts of the appropriate and effective pollinating bees (van der Gross, 1993; Momose et al., 1998). The feeding anthers pump out their pollen towards the bees' mouthparts and thorax, while the fertilizing anthers pump out their pollen onto the bees' parts that come into close touch with the stigma and that are not accessible during pollen grooming. The specialization in the functions of bimorphic anthers and the placement of pollen of each type of anther morphs on different parts of the bee body indicates that *M. malabathricum* with color dimorphism in androceia has evolved for achieving extreme efficiency in cross-pollination however, the plant's ability to maintain self-compatibility facilitates vector-mediated self-pollination. Therefore, *M. malabathricum* is facultative xenogamous but principally out-crossing which is mediated by carpenter bees.

Fruit is a berry-like capsule with numerous seeds enclosed in dark purple, sweet astringent pulp and covered with bristle-tipped calyx. It breaks open irregularly when ripe to expose the seeds. Seeds are dimorphic, one with embryo and another without embryo. Fertile seeds with embryo are spiral and D-shaped in outline while sterile seeds without embryo are also similar to the fertile ones but smaller in size and wrinkled with black test a. Birds eat berries and disperse seeds. Rainwater also disperses seeds during rainy season.



Figure 2 *Melastoma malabathricum*: a. Habit, b. Twig with flower, c. & d. *Nomia* sp. collecting pollen.

Mimusops elengi

M. elengi is a medium-sized glabrous evergreen tree species found in the tropical forests of South Asia, Southeast Asia and northern Australia. It is commonly called "Bullet wood" due its bullet-shaped fruits. Its timber is highly valuable. The fruits are edible. It is highly valuable for its shade, scented flowers and elegant appearance. It is highly valued in traditional medicine. Almost all parts of this tree are used to cure and heal different disorders or ailments (Gami et al., 2012). Anonymous websites reported that *M. elengi* is planted as an ornamental or avenue or shade tree. The bark is used as febrifuge while the leaf is used as antidote for snakebite. The bark and seed coat extracts are used along with extracts from other plant species in herbal tooth powder "Vajradanthi" for strengthening gum of teeth. The flowers are distilled for perfume making due to their fragrance; they are also used for worship to God and for making garlands to decorate women's hair.

The flowering occurs during March-June (Figure 3a). Mature buds bloom at twilight hours and emit a pleasant aroma through the night and the flowers retain the scent even after they fall from the plant and emit scent for several days. Reddi and Janaki Bai, (1981) also mentioned that *M. elengi* is nocturnal in anthesis and the flowers produce strong fragrance. The bark is very thick, smooth, scaly and grayish black. The leaves are petiolate, alternate and oval-shaped with wavy margins and pointed tip. The flowers are borne in axillary clusters, pedicellate, small, creamy-white, star-shaped, hairy, strongly scented and bisexual. They are borne in small clusters in leaf axils. The calyx has 8 lobes in two whorls, the outer whorl with ovate-lanceolate lobes and the inner whorl with 4 narrow lanceolate ones. The corolla is short-tubed with 8 petals, creamy-white and each petal with 2 side lobes and combined into a star-like corolla with a total of 24 lobes. The corolla with all its lobes falls off as a single ring. The stamens are 8 with short filaments, fertile and alternated with 8 staminodes and placed opposite to the inner circle of lobes. The ovary is 2-ovuled and appressedly silky-pubescent with a short style and obscure stigma. The flowers are nectariferous and produce prominent volume of nectar around the ovary. Its production is an indication that the plant is vector-dependent as nectar is offered as a reward for pollen vectors in return for pollination effect.

Reddi and Janaki Bai, (1981) reported that *M. elengi* is wind-pollinated and bees visiting its flowers do not have any role in pollination. Sukri et al., (2021) reported that *M. elengi* is an obligate out-crosser. Its floral traits indicate adaptation for insect-pollination. Different insect species and even sunbirds visit the flowers for nectar and/or pollen but only two bee species *Xylocopa confusa* and *Heterotrigona itama* have highest potential as pollinators in effecting cross-pollination. In this study, *M. elengi* was found to be regularly visited by bees, *Apis dorsata* (Figure 3b) and *Xylocopa pubescens* (Figure 3c), the wasp, *Eumenes conica* (Figure 3d) and occasionally by an unidentified moth (Figure 3e). Of these, the bees visited the flowers for pollen and nectar collection while the wasp and the moth visited the flowers for nectar only. The way the flowers were probed by these insects resulted in pollination due to contact between the body parts of the insects and the floral sex organs. Therefore, this study rules out the report by Reddi and Janaki Bai, (1981) that the bees have no role in the pollination of this plant species.

In Sapotaceae family, fruits of different species are fleshy and edible for animals such as birds, marsupials and bats. vander Pijl, (1957) reported that *M. elengi* fruits are dispersed by bats. In this study, it is found that *M. elengi* fruits mature during July-September period. The fruit is a 1-seeded fleshy bullet-shaped berry, elliptic; it is green initially and yellow when mature and ripe. The fleshy part of the berry is edible and it is used by birds during day time and bats during night time; in this feeding process, they acted as seed dispersal agents of this plant species. Therefore, *M. elengi* is both ornithochorous and chiropterochorous.



Figure 3 *Mimosa elengi*: a. Tree in flowering phase, b. *Apis dorsata* approaching the flower for forage collection, c. *Xylocopa pubescens* collecting nectar, d. *Eumenes conica* collecting nectar, e. Unidentified moth collecting nectar.

4. CONCLUSIONS

W. indica is an herb, *M. malabathricum* shrub and *M. elengi* an evergreen tree. All three species are seasonal bloomers but flowering and fruiting can occur year-long in wet habitats in case of *W. indica* and *M. malabathricum*. All three species are hermaphroditic and

homostylous in which both male and female sexes are functional. *W. indica* shows anthesis from morning and until early afternoon while *M. malabathricum* shows anthesis at sunrise; anther dehiscence is longitudinal in *W. indica* and poricidal in *M. malabathricum*. *M. elengi* is a nocturnal bloomer and dehisces anthers longitudinally. In *M. malabathricum*, heteranthery is functional with yellow anthers acting as feeding anthers and purple anthers as pollinating anthers. Pollinators include *Apis cerana*, *Pachliopta aristolochiae*, *Papilio crino* and *Delias eucharis* in case of *W. indica*; *Xylocopa latipes*, *X. pubescens* and *Nomia* sp. in case of *M. malabathricum*; and *Apis dorsata*, *X. pubescens*, *Eumenes conica* and an unidentified moth in case of *M. elengi*. The study indicates that all the three species are insect-pollinated. Fruit is a 1-seeded dehiscent capsule in *W. indica*, many-seeded berry-like fleshy capsule in *M. malabathricum* and 1-seeded fleshy bullet-shaped berry in *M. elengi*. Hydrochory, zoochory and anthropochory are functional in *W. indica*, ornithochory and hydrochory in *M. malabathricum* and ornithochory and chiropterochory in *M. elengi*.

Authors' contributions

Both authors contributed equally.

Ethical approval

The ethical guidelines for plants & plant materials are followed in the study for collection & identification.

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Conflicts of interests

The authors declare that there are no conflicts of interests.

Data and materials availability

All data associated with this study are present in the paper.

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